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NOTES AND LITERATURE

RECENT LITERATURE TOUCHING THE QUESTION OF SEX-DETERMINATION

In 1889 Geddes and Thomson in their book on the "Evolution of Sex" stated that "Nutrition is one of the most important factors in determining sex" (p. 47), and developed the theory that "Anabolic conditions favor the preponderance of females, katabolic conditions tend to produce males" (p. 47). In the revised edition of 1901 practically the same idea is stated thus: "The female is the outcome and expression of relatively preponderant anabolism, and the male of relatively preponderant katabolism" (p. 140). The following year (1902) Beard¹ expressed the conclusion, based upon considerable evidence, that: "Any interference with, or alteration of, the determination of sex is absolutely beyond human power. To hope ever to influence or modify its manifestations would be not less futile and vain than to imagine it possible for man to breathe the breath of life into inanimate matter" (p. 763).

The two fundamental ideas here expressed—namely, that the nature of the environment (chiefly the amount of nutrition) may determine the sex of the developing germ, *i. e.*, that sex is quantitatively determined; and that sex is predetermined in the germ, *i. e.*, qualitatively (independently of external conditions if only they be favorable to development) have until recently sharply divided investigators on the problems of sex. Both positions seemed about equally well supported by numerous facts both experimental and cytological for animals, and experimental for plants. In only a few instances has opinion been divided over the same form; in the majority of cases the results appeared convincingly in favor of one or the other view.

The more recent tendency seems to be to interpret sex-determination (at least proximately) as the result of a quantitative relation between karyoplasm and cytoplasm in the fertilized ovum, or more strictly, between chromatin and cytoplasm. This position rests upon the observation chiefly that in those insects where heterochromosomes have been described the eggs which develop into females contain the greater amount of chromatin material (exceptions—*Metapodius*, Wilson; and possibly *Acholla*,

¹ Beard, John, "The Determination of Sex in Animal Development," Jena, 1902.

Payne), and has been suggested as probable more particularly by Morgan and by Wilson. The former,² however, regards the quantitative interpretation of sex-determination as only the "first rough approximation" (p. 348) to the solution; and the latter³ inclines to the belief that "if the idiochromosomes be sex-determinants their difference is probably a qualitative one" (p. 189), though this may possibly be a difference merely of degree of special activity.

Boveri's⁴ generalization that the cytoplasm and nucleoplasm of cells bear to each other a constant ratio, and that "a fertilized egg that contains more chromatin is a potentially larger cell than one with less chromatin" (pp. 9-10) may help to reconcile the conflicting theories. If the amount of chromatin may be rightly taken as an index of the state of nutrition or potential anabolic capacity, the apparently contradictory facts that nutrition (environment) in one case and internal factors (perhaps simply more or possibly more active chromatin) in the other case determine sex, can be harmonized. If chromatin and chromatic substances (nucleo-proteids) may be regarded as food material or active agents in constructive metabolism, the better nourished gametes (or such as contain more chromatin) appear destined to produce the female sex, the less well nourished the male sex.

Several recent investigations again affirm the opposing views, well supported with experimental or cytological facts, though a reconciliation is suggested from both sides on the basis of a quantitative relationship signifying in one direction high metabolism (anabolism) and in the other low metabolism ("relatively preponderant katabolism").

The most important recent paper concerning the question of the determination of sex is that of Russo.⁵ This author takes issue with the prevailing hypothesis which views the chromosomes as the vehicles of the determinants of hereditary characters, and objects more especially to a Mendelian interpretation of

² Morgan, T. H., "A Biological and Cytological Study of Sex Determination in Phylloxerans and Aphids," *Journ. Exp. Zool.*, Vol. 7, no. 2, 1909.

³ Wilson, E. B., "Studies on Chromosomes, V." *Journ. Exp. Zool.*, Vol. 6, no. 2, 1909.

⁴ Boveri, Th., "Ueber Beziehungen des Chromatins zur Geschlechts-Bestimmung," *Sitz. Phys. med. Gesell. Wurtzburg.*, Jahrgang 1908-1909.

⁵ Russo, A., "Studien ueber die Bestimmung des weiblichen Geschlechtes," Jena, 1909, pp. 1-105.

sex-phenomena. The fact that in the gametes, particularly the eggs, besides certain phosphorus-containing proteins, lecithin is abundantly present, suggested a series of experiments to determine whether the lecithin content of eggs could be artificially increased and whether such accession could produce a significant physiologic modification in the germ-cells.

Russo finds that normally in rabbits and various other mammals the lecithin content of eggs of the same ovary varies greatly; some containing much, others little. This variable cell condition indicates a shifting chemical state, expressed morphologically in the form of "chromidial-bodies" (mitochondria, chondriomites, pseudochromosomes, chromidial net, etc.). These structures Russo has succeeded in producing by artificial means (*i. e.*, injection of lecithin), and he regards them as having "no small influence on developmental phenomena." He does not deny that the nuclear chromatin plays an important rôle in development, but he refuses to regard it as alone the material basis of heredity. The nuclei may assist in the process of heredity, but the results of his investigations on rabbits indicate that sex and other "unit characters" (*e. g.*, pigmentation) are a function of the degree of cell metabolism.

Russo believes that "contrary to the chromosome theory, the characters of Mendelian hybrids in the first or dominant generation, especially as concerns the pigmentation and color of the hybrid, do not bear any absolute relation to the chromosomes, but that they depend in greatest part upon a specific metabolism or chemical condition residing in the egg cytoplasm; that, further, the sex of the offspring depends upon a special metabolism (*Stoffwechsel*) of the germ-cells, and that by artificial modification of the chemical or metabolic state (*Metabolismus*) of these elements the Mendelian law (*i. e.*, of dominance) can be modified in that one may fix this or that most recent variety, as it is also possible at will to determine the sex" (p. 4).

Lecithin was administered subcutaneously, intraperitoneally and per os. The ovaries of lecithin-fed rabbits attained a size three times as great as that of ordinary individuals and contained much larger Graafian follicles. Under such treatment the germ cells became markedly anabolic. Russo notes that in normal ovaries some ova contain much deutoplasmic material in the zona pellucida and the vitellus, and others little or none. The artificially highly nourished eggs produce females; and the lecithin-fed individuals give rise preponderatingly or even ex-

clusively to female offspring. There are thus in rabbits two kinds of eggs corresponding, respectively, to each sex: (1) well nourished, highly anabolic, or female; (2) poorly nourished, slightly anabolic (or katabolic) or male.

The sperm, containing chemical substances similar to the eggs, are regarded as merely giving aid in the development of a process already begun in the egg leading towards the determination of a particular sex. That the sperm has a complementary and not an antagonistic rôle in sex-production seems established by the fact that the percentage of female offspring is higher when both male and female have been subjected to the lecithin treatment before union.

For the experiments Russo employed selected and ordinary varieties of rabbits. His chief aim was to "fix" a particular "unit character" of the female in the offspring (mostly female) of the first hybrid generation. The character selected was the color of the hair. Females of recent races characterized for hair color, *i. e.*, white (albino, Himalaya, Angora, etc.), were crossed with males of various phylogenetically older races (*e. g.*, "Grigia"—gray, and "Nero"—black). The best results were obtained from crosses between Himalaya females and "Nero" males. On crossing females of either albino or Himalaya races with males of "Grigia" and "Nero" stocks the offspring of the first generation always had the color of the male, *i. e.*, gray or black, respectively, showing that these crosses ordinarily conform to the Mendelian law of dominance. Moreover, Russo notes that in nature the number of male offspring always exceeds that of the female, the percentage of the former being variously given as from 52 to 58 per cent.

When the same females were subjected to the lecithin treatment before conception, the offspring of crosses similar to the above were in the first generation preponderatingly of the type of the newer or female race. There frequently appeared atavistic exceptions, interpreted as due to a late ripening of the eggs concerned which consequently remained unaffected by the lecithin.

The most clear-cut result was obtained from the following experiment: A preliminary experiment, several times repeated, having shown that the ordinary cross conformed to the law of dominance, a young well-nourished "Polacca" (white) lecithin-treated female was crossed with a "Nero" male (black). The resulting progeny included 6 females (5 white) and 2 males (1

white), showing clearly that the female subjected to lecithin treatment yields a preponderance of females (with the maternal somatic character of hair color).

Occasionally the cross between a lecithin-fed Himalaya female and a normal "Nero" male resulted in several modified Himalaya offspring (*e. g.*, black legs or dusky coat, etc.) among the preponderating Himalaya hybrids. This condition is readily explained by assuming that in such crosses "the modification of the vitellus had not reached the necessary stage to impress upon the embryo the character of the maternal metabolism and with it the characteristic female features" (p. 16).

The cause of the concomitance of sex and particular somatic characters is believed by Russo "to depend upon a suitable modification of the germ-cell, related in some way to the age, the physiologic state and other conditions of the particular individual" (p. 98).

The evidence here appears unequivocal that external conditions (*e. g.*, nutrition) can determine the kind of sex and entirely vitiate the Mendelian scheme of ordinary crosses. Female sex and the maternal character of coat color moreover are shown to be associated with a more highly nourished egg, the artificially modified metabolism expressing itself in an abundance of deutoplasmic and chromatic substances (chromidial-net) in the zona pellucida and vitellus. The main stages in the chain of causes culminating in female sex seems to be, (*a*) high nutrition (lecithin), (*b*) increased size (preponderant anabolism), (*c*) storage of chromatin, (*d*) femaleness.⁶

A brief paper by Miss Boring⁷ gives the results of a careful study of fertilized eggs of *Ascaris* with special reference to the

⁶ The relation of nutrition to sex-determination as demonstrated by Russo for the rabbit suggests a possible physiologic basis for the theory of sex-causation in man (based solely on clinical facts) as recently advocated by Dawson to the effect that females develop from eggs from the left ovary and males from eggs from the right ovary;—namely, that the permanent passive congestion in the left ovary, due to the entrance of the left ovarian vein at a right angle into the renal vein (whereas the right ovarian vein empties obliquely directly in the inferior vena cava) may produce a condition of relatively better nutrition. Cognizance must be taken of the fact, however, that the right ovary is frequently slightly larger than the left, a point which apparently contradicts the verity of this interpretation; but cytological investigation may reveal a better nourished condition of all of the ova of the left ovary, expressed in the presence of chromidial nets, etc.

⁷ Boring, Alice M., "A Small Chromosome in *Ascaris megalcephala*," *Arch. f. Zellforschung*, Bd. 4, H. 1, 1909.

small odd chromosome previously noted by Herla and later also by Boveri. This peculiar chromosome is said to be very rare in the variety *bivalens*. Its representative was never discernible in the oögonia and only very rarely in the spermatogonia. From observations of bastard eggs the conclusion is drawn "that the small chromosome surely comes from the spermatozoön in some cases, and possibly from the egg in others" (p. 125—one instance noted). The possibility is suggested that the small chromosome is a sex-determining heterochromosome; but Miss Boring has no doubt also that it is sometimes due to fragmentation.

Boveri⁸ inclines to regard this fifth ("X")—chromosome of *Ascaris megalocephala bivalens* (present in approximately half the eggs) as comparable to the accessory chromosome of *Pyrrhocoris*. He considers it more probable that its occasional apparent absence (common condition in *univalens*) is the result of fusion with one of the other chromosomes, than that its presence is the result of fragmentation. He concludes that the "x-chromosome" appears to be an independent structure specific for the male sex—as was originally believed by McClung for insects. In analogy with conditions in insects (*e. g.*, *Protenor*), Boveri assumes a dimorphism of spermatozoa, due to the presence of the x-element in half of the sperm and its absence in the other half. But the unfertilized eggs are supposed to have no homologous elements (there being no evidence of such structures); hence, contrary to his recent generalization that the female fertilized egg contained the greater amount of chromatin, the male sex here seems conditioned by, or concomitant with, a relative preponderance of chromatin. This contradiction is elucidated by facts discovered by Boveri and Gulick (*op. cit.*, p. 136) in a study of the spermatogenesis and maturation of *Heterakis*, a nematode of the pheasant. The spermatogonial cells have 9 chromosomes; the maturation spindles of the eggs 5. Two types of spermatids are produced, one with 4 the other with 5 chromosomes; and one kind of egg with 5 chromosomes. The condition is identical with that described by Wilson for the hemipter, *Protenor*.

These facts established for *Heterakis*, give a clue to the more probable state of affairs in *Ascaris*. Boveri reconciles the discrepancies by assuming a close union in the oöcytes of the homologues of the accessory chromosome with the other chromosomes thus masking their presence. In reality, then, *Ascaris mega-*

⁸ Boveri, Th., "Ueber 'Geschlechtsschrosomen' bei Nematöden," *Arch. f. Zellforschung.*, Bd. 4, H. 1, 1909.

Locephala bivalens would have six (6) chromosomes in the female and five (5) in the male (apparently four (4) in each since the heterochromosomes commonly couple with the ordinary chromosomes).

The attempt to rationalize the assumption of such a union involves the hypothesis of chromosome individuality in extreme form, viz: "We can not doubt that also in the apparently homogeneous nucleus of the spermium each chromosome preserves its individuality; but all are most closely pressed together" (p. 139). The greater effort here demanded (as compared with the egg pronucleus) to separate the chromosomes in this more compressed condition affects also the odd chromosome and frequently disjoins it from its "companion."

Thus two more forms (from the group of the Nematodes) are shown to conform to Wilson's scheme of sex-determination. And though Boveri is forced to retract (p. 137) his former statement regarding a preponderance of chromatin in the female sea-urchin as judged from Baltzer's plates the evidence accumulates that the female sex is somehow associated with a greater amount of chromatin.⁹

In an extensive paper of 110 pages on sex-determination in *Polyps*, Nussbaum¹⁰ describes in detail a large series of experiments extending from 1891 to 1897 on *Hydra grisea*. His discussion of results involves comparisons with the works principally of Krapfenbauer (*H. fusca*), Frischholz (*H. fusca* and *H. grisea*), Whitney (*H. viridis*) and Annandale (*H. orientalis*).

The aquaria were all arranged under similar conditions of light and heat; only the nutritive conditions were caused to vary by changes in the amount of food supply and by induced periods of budding. The temperature is said to have an effect on sex only indirectly through influence on the nutrition. In contradistinction to the four above-named investigators, Nussbaum maintains that the nutrition and not the temperature is the chief factor which determines change from the asexual or budding condition to the sexual (diceious and hermaphrodite); though he agrees with the latter two that for each species there is a definite temperature-optimum.

⁹ The case of *Acholla multispino*a described by Payne (*Biol. Bull.*, Vol. 16, nos. 3 and 4, 1909) may perhaps prove a real exception, though it may be harmonized, as Payne suggests, by assuming a greater combined activity for the several smaller "differential chromosomes," than for the single absolutely larger male member.

¹⁰ Nussbaum, M., "Ueber Geschlechtsbildung bei Polypen," *Arch. (Pflüger) f. Physiologie*, Dec. 30, 1909, Bd. 130.

With good feeding budding gives place to a sexual phase. On the basis of daily observations of many cultures for a number of years Nussbaum concludes that a more favorable nutritive condition produces the female polyp. "The mass of food governs budding and the production of sexual organs"—and the best nutrition produces females. The same polyp may enter upon repeated sexual phases each separated by a period of budding; but, while he seems to deem it possible, he has not yet succeeded in changing the sex of the same individual polyp directly into the opposite sex.

Here again the same general conclusion appears that sex is consequent upon the degree of nutrition and that the best nourished polyp produces eggs, *i. e.*, high nutrition conditions the female sex.

Nussbaum suggests an interesting new interpretation of hermaphroditism (gynandromorphism) among insects where a dimorphism of spermatozoa prevails, *i. e.*, where heterochromosomes are found. He believes it quite possible that occasionally the reducing division may be omitted in spermatogenesis and that the unmaturred spermatocytes may develop directly into functional sperm. Shortly before, or at the time of, the first segmentation of an egg fertilized by such a spermatozoon, the male pronucleus is supposed to undergo its belated reduction division, one half (with the even number of chromosomes) passing to one daughter cell with one half of the developing egg pronucleus, and the other half (with the odd number of chromosomes) with the other similar half to the other cell. Thus would result a two-cell stage, one blastomere (female) containing one more chromosome than the other blastomere (male). If then, as has been experimentally demonstrated in several forms, each blastomere gives rise to one half of the resulting individual the symmetry of the insect hermaphrodite would be explained. Here again sex is thought of as determined by a quantitative relation of chromatin.

The results of the newer investigations on sex-determination seem, at least temporarily, to have brought us back to the position of Geddes and Thomson, namely, that femaleness is causally related to a dominating cell-anabolism and maleness to a relatively preponderant cell-katabolism. This conclusion would seem to be the base from which future investigations will start in the attempt to further elucidate the fundamental mechanism of sex-differentiation.

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